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FURTHER OBSERVATIONS ON THE POSE OF THE SAUROPODOUS DINOSAURS

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SINCE the publication[1] of my paper on the manner of locomotion of the Sauropoda a number of communications have appeared which treat of the same subject. Two of these I wish especially to notice here, both of which have appeared in the AMERICAN NATURALIST, one of these being written by Dr. W. J. Holland;[2] the other by Dr. W. D. Matthew.[3] A third interesting and instructive paper, from the pen of Dr. O. Abel, appeared in March, 1910, in the *Abhandlungen der k. k. zool.-botan. Gesellsch. in Wien,* Volume V, Heft 3, pp. 1–60.

Dr. Holland experiences many difficulties in his attempts to articulate the bones of *Diplodocus* so as to give the animal a pose like that of the crocodile and of the lizard. His Fig. 9, on page 268 of his communication, is intended to illustrate some of his perplexities. "Of what earthly use," he says, "the hind limb of the *Diplodocus* could have been to him in such a position I leave you to determine for yourselves." Now, although the proximal ends of those femora are not all placed as they are in the lizard or the crocodile, nevertheless, taking them as Dr. Holland has placed them, it is difficult to see why, if they were not ankylosed with the pelvis and the animal had not contracted locomotor ataxia, it could not lift itself out of the hole provided for it. Furthermore, it is not necessary for lizards to carry their knees above the level of their backs; no more was it necessary for sauropods to do this. Dr. Holland finds trouble also at the knee-joint, when the leg is flexed, as shown in his Fig. 11, in which case, as he states, the tibia and the fibula come into contact with the condyles of the femur at two points not larger than as many sixpences. But we must suppose that the *Diplodocus* did sometimes lie down, and in so doing did bend its legs as much as Dr. Holland has represented, or more. Whoever has observed the effort required by a horse in regaining a standing posture can imagine the strain that would come on those femoral condyles and lower leg bones when the reptile endeavored to get on his feet again; but we can hardly suppose that the bones and cartilages of the knees were crushed every time the animal arose from its slumbers. Dr. Holland appears not to appreciate the fact that all these articular surfaces were invested with abundant cartilage.

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[1] *Proc. Washington Acad. Sci.,* XII, 1910, pp. 1–25.

[2] AMER. NATURALIST, XLIV, pp. 259–283.

[3] AMER. NATURALIST, XLIV, pp. 547–560.

Dr. Holland's Figs. 15 and 16 illustrate the embarrassments encountered by him in his efforts to adapt the bones of the fore leg to the positions that they have in the lizard. He would have had fewer difficulties had he not been laboring under the misapprehension that the upper end of the radius articulated with the inner condyle of the humerus instead of the outer. Such a transposition of the radius and ulna would present something unique in anatomy and, in the case of the sauropods, would be wholly unnecessary.

From the compressed form of the body of *Diplodocus* Dr. Holland has derived an argument against the proposition that the reptile had a creeping mode of locomotion. Dr. Abel also formulates the generalization that among the reptiles which in locomotion do not lift the belly and thorax from the ground but drag it, the cross-section of the thorax is transversely oval. It is true that most creeping animals have the body depressed, but they vary greatly with respect to the amount of depression. On the other hand, there are lizards which have the body strongly compressed and which nevertheless progress as do other lizards. A species of the genus *Gonyocepha-*

lus shown me by Dr. L. Stejneger has the thickness of the body only .57 of the height; so that it is nearly as much compressed as Dr. Holland has represented *Diplodocus* to be. Various other genera of lizards include species with much compressed bodies. Some of the tortoises belonging to the genus *Testudo* have the shell about twice as wide as high, while in *T. abingdonii,* from the Galapagos Islands the shell is fully as high as wide. Nevertheless, this tortoise shows no tendency to assume a mammalian gait. I see no reason why, if the necessities of the animal required it, the shell might not, in the course of time, become still higher.

It is of great value to have, from one so competent as Dr. W. D. Matthew, a statement regarding the value to be attached to the form of the femur in relation to the pose of the sauropods. Dr. Matthew seems to agree with me that straightness alone of the femur does not prove that these animals walked erect on either two or four legs, only, he appears to hold that the larger mammals and dinosaurs have in general straighter femora than their smaller and more agile ancestors. This statement is, of course, subject to the condition that the femur was not straight in the ancestors themselves. And when we come to apply the statement to the dinosaurs we are likely to dispute whether the femora of *Tyrannosaurus* are or are not less curved than those of some earlier dinosaurs. Dr. Matthew describes the hinder limb of the elephant and asserts that all gigantic mammals show some approach to this type; also, that in the sauropods the resemblance in form and proportion of the hinder limb to that of the elephant is very marked. However, a number of the genera that he mentions as illustrating his views seem to me not to conform well to the specifications. *Titanotherium* does not, if we may rely on the restorations,[4] have post-like legs nor, in comparison with the elephant, short feet. *Coryphodon* does not have straight legs,[5] nor is it a gigantic mammal, being exceeded in size by some of the rhinoceroses, which again have very angulated legs. It is to be noted, too, that most of the genera mentioned by Dr. Matthew as being gigantic mammals of diverse stocks are extinct, and there might be some differences of opinion as to the exact form of their legs and even of the feet.

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[4] *Bull. Amer. Mus. Nat. Hist.,* VII, pls. VIII, X, XI.

[5] *Bull. Amer. Mus. Nat. Hist.,* X, pl. X.

Nor is it certain that the type of limb found in the elephant is the result of the great size of the animal. The limb has probably not changed greatly since Middle Eocene times, when elephants were small animals; although its angulation has probably become somewhat reduced, the femur relatively somewhat longer, and the digits a little shorter. The femur of *Mœritherium,* supposed to be a relative or even an ancestor of the elephants, from the Middle Eocene of Egypt, is only eleven inches long and is as straight as that of the living elephant. The type of leg possessed by the elephant is rather primitive in its structure and is found in such animals as are slow of movement. All animals have some means of protecting themselves more or less effectively from their enemies. Horses, deer and oxen have developed angulated limbs, with short humeri and femora and elongated metapodials, combinations that confer the power of rapid flight. The elephants have found their safety in their great size; and extensive modifications of their legs have not been required.

As is well known, the lizards have straight-shafted femora, which are longer than the tibiæ, and the digits are long. As, however, the land tortoises may have short digitigrade feet, it is difficult to see why some lizards might not develop such feet. And it is not improbable that such a lizard might attain a great size and continue to retain its straight femora, short feet, and angulated limbs.

In short, it seems to the writer that Dr. Matthew's proposition as regards the significance of the straight femur is loaded with so many conditions and subject to so many exceptions, known and supposable, that it must be applied with great circumspection to the dinosaurs.

It is frequently asserted that the pelvis and the limbs of the diplodocus possessed analogous resemblances to those of the elephant. In the pelvis these are confined, I believe, to the great size and to the convex iliac crest. In the sauropod the ilia are directed from front backward; in the elephant almost transversely. The pubes and ischia in the two animals are utterly different. The acetabula are different in form, size and position. The femora of the two animals are alike large and straight-shafted. That of the sauropod, however, has no great trochanterial process; and whether, as my critics contend, only the inner angle of the proximal end of the femur or, as I insist, the whole of the proximal end, is to be regarded as the head of the bone, this head is very different from that of the elephant. The size of the radius relatively to the ulna and of the fibula to the tibia is very different in the two animals. The digits of the elephant, in general, are far less reduced than those of the sauropod. That the limbs of the sauropods were straight like those of the elephant has been assumed; but we are now discussing that proposition.

On the outer border of the upper end of the femur of *Diplodocus* is a rugose area which extends downward a distance equal to one fifth the length of the bone, perhaps somewhat more. This, or at least its lower end, represents the trochanter major. According to Dr. v. Huene's figures, this trochanter occupied about the same level in the Triassic dinosaurs, but it was placed somewhat more on the dorsal surface of the bone. Osborn[6] represents this trochanter in approximately its correct position, but not extended far enough downward, as is evident from the photograph reproduced on his Plate XXIV. Dr. Matthew speaks of this trochanter as a "clearly marked rugosity around the proximal external angle of the head." I find this rugose surface on other sauropod femora. The upper half of a large femur in the U. S. National Museum measures 510 mm. across the bone just below the rough proximal end. On the fibular border the rugose surface that represents the great trochanter runs down on the bone a distance of 390 mm. At this point there is a decided angle in the border on the bone. A rough surface just like this in position and extent is found on the femur of the crocodile.

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[6] *Mem. Amer. Mus. Nat. Hist.*, I, p. 210, Fig. 14.

This being settled, we may turn our attention to what Marsh and Hatcher called the great trochanter, the outer half, or nearly as much, of the rough proximal end of the femur. Those who do not believe that this formed a part of the head of the bone and was not inserted in the acetabulum ought to explain what it represents.

As regards the distal end of the femur of *Diplodocus,* I do not see in what way it is essentially different from that of the lizard. Dr. Matthew says that in the latter the distal articulation for the tibia and the fibula are on the back of the femur, not on its end. As I see the femur of *Diplodocus* and that of the lizard, both have a broad articular surface on the end; and this surface is continued around on the ventral side of the bone, being there divided into two parts by the intercondylar fossa. It must not be supposed that I see no differences among the femora of the diplodocus, the crocodile and the lizard; but these are much nearer one another than that the diplodocus is to the femur of the elephant.

Dr. Holland has made the objection that in articulating the leg bones of *Diplodocus* so that there might be a right angle between the femur and the tibia there would be no surface against which the end of the femur might articulate. However, the same condition would exist in the flexed knee of the horse or of man were it not for the patella. In the flexed knee of the lizard and of the crocodile the end of the bone is covered by the tendon of the extensor muscle and the ligaments; and certainly the same was true in the sauropods. On account of the deep body of *Diplodocus* it would not probably often happen that the angle between the femur and the tibia would be less than a right angle. When the leg was extended forward it would be nearly straight and again straight when directed backward. Also, the body would be lifted somewhat. It is an erroneous idea, held apparently by both Dr. Matthew and Dr. v. Huene, that in walking the crocodiles, lizards and turtles do not lift the body from the ground. Probably all do so; even the gigantic Galapagos tortoises carry their bodies free from the ground.

Inasmuch as the arrangement of the bones of the fore leg has been brought into this discussion, I shall make a few remarks on the subject. Few of the figures of the humerus give a correct notion of its form. Those published by Osborn and Granger[7] show well the characters of the bone, seen from the front only, in three genera of sauropods. A humerus in the U. S. National Museum, supposed to be that of *Diplodocus*, has the proximal border broad and convex and very rough, showing that it was covered by cartilage and doubtless formed a continuous articular surface. This surface played in the glenoid fossa or notch of the shoulder girdle. About the middle of this convex surface the bone is much thicker than at the ends and the thickening is on the dorsal face of the bone. This thickened portion quite certainly corresponds to a rounded elevation seen on the upper surface of the proximal end of the humerus of the crocodile, and this in its turn is probably homologous with the more narrowly limited head of the humerus in mammals. In the crocodile this elevation fits well into a depression in the scapula, in the roof of the glenoid fossa. When, however, the leg is brought well forward the elevation slips out of the glenoid notch and a part of the head farther forward takes its place and supports the weight. I believe that the same movements took place in *Diplodocus*.

Now, in the restoration of *Diplodocus* in Pittsburgh and in that of *Brontosaurus* in New York, the humerus is placed in the glenoid notch in an approximately vertical position, with the deltoid border directed outward. the opposite border inward, and the primitively dorsal surface directed forward. This leaves the inner, probably lesser, tuberosity projecting far within the inner surface of the shoulder girdle. An examination of a lot of mounted skeletons will show that in all mammals that walk by moving the limbs in sagittal planes the inner tuberosity is greatly reduced and removed to a position in front of the head of the bone, and little or none of the humerus projects beyond the inner surface of the scapula. In two mammals I find a large process which corresponds, in position at least, to the inner one of the sauropods. These are the echidna and the duck-bill, and both of these mammals move the legs as the creeping reptiles do. I believe that the prevailing manner of articulating the humerus of the sauropods is wrong. It ought to be placed in a plane approximately horizontal, with the lower and upper faces in their primitive positions, with the deltoid border forward, and, when the leg is in a median position of its swing, with the thickening of the proximal articulatory surface in contact with that part of the glenoid notch that is formed by the great ridge that passes across the scapula. In case the leg is placed further forward or further backward, corresponding parts of the convex articular end of the humerus ought to pass under this ridge. There was no need at any time of life that the lesser tuberosity should project against the ribs or into the muscles. The arrangement that I have described is that which may be observed in the crocodile also.

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[7] *Bull. Amer. Mus. Nat. Hist.*, XIV, p. 203.

If now the ulna and the radius are articulated properly with the humerus the whole leg will function as it does in the lizard and the crocodile. In the U. S. National Museum is a specimen, shown me by Mr. Chas. W. Gilmore, which consists of the radius and the ulna, somewhat crushed, but preserving nearly their original relations to each other. These bones differ somewhat from those of the crocodile, as might be expected. The principal difference is found in the fact that the upper end of the ulna extended across the lower end of the humerus and has a concavity in front for the head of the radius. The ulna and radius appear to have been more closely bound together at the lower ends than in the crocodile; nevertheless, the bones of the two reptiles resemble one another closely. When to those of the sauropod a humerus of corresponding size is fitted, with the outer (anterior) condyle in contact with the head of the radius, the leg is strikingly like that of the crocodile. In my opinion, Marsh's arrangement of the bones of the fore leg of *Brontosaurus*[8] is more nearly correct than later restorations of this limb in the same animal and in *Diplodocus*. In the figures referred to, the humerus, in the middle of the step, presents the dorsal surface outward; whereas, in the Pittsburgh and New York restorations this surface looks backwards and the deltoid border looks outward. If Marsh's figure were modified so that the humerus were horizontal or nearly so, the leg would have nearly its natural position.

Various opinions are held regarding the question whether the sauropods were strictly aquatic, strictly terrestrial or amphibious. In my paper published in the *Proceedings of the Washington Academy of Science* I called attention to a figure that illustrates Cope's views and to another published by Matthew that elucidated Osborn's ideas. Dr. Matthew's views seem to differ from those of Osborn in that the former maintains that these reptiles usually preferred not to be wholly submerged and that they could not leave the water without endangering the integrity of their limbs. He finds his reasons for his opinion as to the depth of the water preferred in the fact that the bones above a line drawn from the hip joint to the shoulder blade are of light construction, while those below this line are thick and heavy. This line is his "water-line" and indicates the average depth of the water haunted by these reptiles. The heavy bones of the legs were intended, according to Dr. Matthew, to hold the animal down in the water, as the lead in the diver's shoes holds him on the bottom. However, it occurs to the present writer that if the sauropods were accustomed to wade in water that came only a little more than halfway to their backs the weight of the unsubmerged part of the body would suffice to hold them to the bottom. A man who wades in water only waist-deep does not need leaden soles. To maintain the theory, it seems necessary to keep the reptiles more deeply submerged. To do this it is only necessary to suppose that they crawled about at the bottom of the water as crocodiles do. If we suppose that the sauropods walked wholly submerged and erect on four legs the differentiation observed by Dr. Matthew in the ossification might be explained on the supposition that it was for the purpose of ballasting the animals. However, it does not appear that the hippopotamus, an eminent wader, needs to be steadied in this way. Furthermore, why should it have disturbed such facile swimmers as the sauropods probably were to heel over occasionally?

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[8] The Dinosaurs of North America, Pl. XLII.

Notwithstanding the means employed by nature to reduce as much as possible the weight of the skeleton, the bodies of the sauropods were very heavy. The bones of the legs were well-developed and I recognize that they were not as hollow as those of a horse, for example. Can we not, after all, most reasonably explain the case by supposing that the sauropods went about more or less on land and needed strong legs to hold up their heavy bodies?

In my former article I expressed the opinion that it was hardly possible for a diplodocus to walk about wholly submerged. It appears that Cope and Osborn and Matthew have thought that the animal would have no difficulty in doing this. Perhaps the question can never be definitely decided. The hippopotamus is said to walk beneath the water and probably does really do so; at least they remain for considerable periods beneath the water and move about. They are active swimmers and it is possible that their movements along the bed of the river or lake are to a considerable extent due to the action of their feet against the water. They have massive skeletons which have evidently been developed to bear them down in the water. Nevertheless, it is to be questioned whether the animal exerts any considerable pressure on the bottom. If the specific gravity were any considerable amount above that of the water the animal would have difficulty in coming to the surface for air and to get a view of its surroundings. Tapirs too are said to be great swimmers and divers and to run along on the bottoms of streams; but these mammals have no special modifications of the skeleton to enable them to do this. Possibly they lay hold of the bottom in some way with their hoofs, or, while running they may incline the head and body downwards and forwards, like a descending aeroplane. That the hippopotamus with his heavy skeleton has a specific gravity little above the water is proved by the following fact related in Brehm's Thierleben: When a hippopotamus is killed he at once goes to the bottom. Nevertheless, in many cases the body comes to the surface within from 30 to 60 minutes, a result of the development of gases within the cadaver. Hence, it is extremely doubtful whether the animal can exert much pressure on the bed of the stream. So too, even if the sauropods did walk about at the bottoms of streams, wholly submerged, they must have rested there very lightly.

Now what conclusions can we draw from the facts above established? Dr. Matthew's strongest argument in favor of the erect pose of the sauropods is derived from the supposed resemblance of their limbs to those of the elephant, the long straight femur, the short digitigrade feet, and the slight angulation of the limb. "Obviously," says he, in describing rectigradism, "a specialization of this kind will occur only in an animal which habitually rests its weight on the limbs." But we are dealing here with animals that are supposed to have the whole, or at least nearly the whole, of the weight taken from their limbs.

Moreover, does not the one part of Dr. Matthew's theory contradict the other? He has told us that the parts of the skeleton below the water-line were heavy for the purpose of overcoming the buoyant effect of the water, as the lead in the diver's shoes does. Then, as shown in the preceding paragraph, he maintains that there was pressure enough to produce such legs as the elephant has, an animal whose legs must support its whole weight.

We may now be permitted to inquire whether or not aquatic life is likely to have produced either of the effects attributed to it by Dr. Matthew. The hippopotamus is an animal far less aquatic than Cope and Osborn and Matthew have supposed the sauropods to have been. Its limbs are almost ridiculously short, so short that when it is quitting or entering the water its belly leaves broad and deep channels in the mud through which it wades. The leg bones are indeed very strong, a result conditioned by the frequent excursions made on the land. The feet are the most primitive possessed by any living artiodactyl, and the digits are bound together by a short web. The aquatic performances of the tapir have not contributed to its structural uplift, for its feet are among the most primitive of those of the perissodactyls. Let one only view with some attention a series of mounted skeletons and one will soon be struck with the fact that degenerative changes begin to affect the limbs of animals very shortly after they begin to confide to the water the support of their bodies; and these degenerative modifications continue to manifest themselves until the limbs have been converted into paddles and flippers or reduced to vestiges or even extirpated.

That the sauropods had originally been amphibious and then became strictly aquatic seems to the writer highly improbable. Those short digitigrade feet, with toes having a reduced number of phalanges, seem to furnish almost positive proof that their possessors had for many generations been accustomed to travel on solid ground. It is probable that their resort to the water had not endured long enough yet to affect to any great degree their organization, except as to size.

Dr. Matthew believes that at some stage the ancestors of the sauropods were bipedal and that later they became secondarily quadrupedal. He grants that the indications of former bipedalism in this group are less apparent than in the quadrupedal Predentata. It is easy to agree with the latter opinion. As to the hinder limbs, we ought to expect that bipedal locomotion would have led to the development of smooth, well-finished articular surfaces and of a trochanter major standing out as a distinct process near the upper end of the femur. Why, on the resumption of quadrupedal locomotion, should these acquisitions have disappeared as if they had never existed? This has not happened even in the walruses, seals, porpoises and manatees, which forsaking the land, have betaken themselves to the water. The inevitable result, if not the prerequisite, of bipedalism is a considerable reduction in the size of the fore legs and various transformations of the hands. But the fore limbs of *Diplodocus* and of *Brontosaurus* show no reduction in size. Are we to suppose too that while the fore legs were held from contact with the ground and were probably employed for other purposes than locomotion, they continued to progress in digitigrady? Those fore feet look as if they had been walked on fully as much as the hinder feet.

From a photograph of the fore foot of a *Diplodocus* in the American Museum of Natural History Dr. v. Huene concludes that this foot was exaxonic. It would be interesting to learn more about this foot, especially whether or not the bones were found in their natural relations. The foot differs from that of some other sauropods, certainly. With the ulna and radius before mentioned, in the U. S. National Museum, there are present all the metacarpals and some of the phalanges. Through pressure two of the metacarpals, the fourth and the fifth, have had their hinder faces squeezed against the hinder faces of the other three. Otherwise, the bones retain their original relationships. Of these the first is distinctly larger than the fifth. The lower end is especially enlarged, to support the phalanx and the great claw. It is proper here to say that Dr. v. Huene has very justly criticized the representation of the feet of *Diplodocus* as presented in my plate published in the *Proceedings of the Washington Academy of Science.*

Dr. Matthew refuses to accept my explanation of the tracks made by the supposed iguanodon. Those tracks are certainly in need of explanation. So far as I am aware, no one has as yet ventured to mount a dinosaur with the toes pointing inward after the manner of those tracks.

Neither does our author accept my suggestion that some of the tracks found in the Triassic sandstones of the Connecticut River Valley were made by birds. The conclusion appears to be that, because a few dinosaur *bones* have been found in that region, therefore all the *tracks* are those of dinosaurs. Dr. Matthew does not attempt to show how animals built as were the Triassic dinosaurs that we know, with short diverging femora, rather short lower leg bones, and short metatarsals, could put one foot directly before the other in walking or running. It is much to be doubted whether a running duck or penguin could do this. And are we to suppose too that those Triassic dinosaurs were always running? It may be easy in mounting the skeleton of a dinosaur to place the femora parallel or even to bring the knees together. In life the thighs could not take this position, unless on each side there had been a considerable excavation at the junction of the ponderous belly and the thick tail, a sort of little wheel-house for the thigh to play in. It seems quite doubtful whether the carnivorous dinosaurs of even the Jurassic period had the erect bird-like bearing that is usually attributed to them. The extraordinary development of the pubic bones of *Ceratosaurus,* whose expanded and ankylosed distal ends reached nearly half-way to the fore legs, seems to me to indicate that these animals, when in repose, had a prone position, resting much of the weight on the pubes, and that when running their legs straddled considerably.

Dr. Matthew thinks that the sauropods had too great a bulk to have lived on land. The law to which he gives expression does, of course, prescribe a limit to the size an animal can attain, but who has yet determined what that limit is? Larger elephants have lived than those now living, and it is not certain that we have discovered yet the largest that have lived. Animals do not attain a great size simply to test the laws of mechanics.